A NEW SPECIES OF FRAGARIA (ROSACEAE) FROM OREGON

Kim E. Hummer

USDA ARS National Clonal Germplasm Repository
33447 Peoria Road
Corvallis, Oregon 97333-2521 U.S.A.
Kim.Hummer@ars.usda.gov

ABSTRACT

Fragaria cascadensis K.E. Hummer, sp. nov. is endemic to the western high Cascade Mountain Range in Oregon, United States. This decaploid species can be distinguished by adaxial leaf hairs, distal tooth of the terminal leaflet always smaller than adjacent teeth, and commashaped achenes. Its known range is in the western Cascade Mountains from the Columbia River in the north, to the vicinity of Crater Lake in the south, at elevations of 1,000 to 3,800 m, in sandy-clay loams of volcanic origin, in forest clearings and open meadows.

RESUMEN

Fragaria cascadensis K.E. Hummer, sp. nov. es endémica de la Cordillera de las Cascadas en Oregón, Estados Unidos. Esta especie decaploide puede diferenciarse por los pelos del envés de las hojas, diente distal del foliolo terminal siempre más pequeño que los dientes adyacentes, y los aquenios en forma de coma. Su rango conocido va del oeste de la Cordillera de las Cascadas desde el río Columbia en el norte, a las proximidades del Crater Lake en el sur, a elevaciones de 1,000 a 3,800 m, en margas arenoso-calcáreas de origen volcánico, en claros de bosque y en parados abiertos.

DESCRIPTION

Fragaria cascadensis Hummer, sp. nov. (Figs. 1–3). Type: U.S.A. Oregon. Lane Co.: US NFDR 5897, southern exposure, disturbed area at forest edge, along roadside ditch, altitude 1433 m, with Pseudotsuga menziesii, 8 Aug 2011, K.E. Hummer CFRA 2111 (HOLOTYPE: OSC 233175).

Plants perennial, acaulescent, crown-forming herb with stolons and adventitious roots; petiole, pedicel, runner and calyx with dense, spreading hairs. Stolons red, sympodial. Leaves generally trifoliate, rarely quadrior pentifoliate; slightly bluish green; adaxial surface with scattered appressed white hairs about 1 mm; not thick or coriaceous, and not reticulate-veiny beneath. Shape of leaflets variable, elongated to obovate, cuneiform or broadly round, truncate; margin variably serrate, entire to only upper third of leaflet; teeth small and pointed, rarely crenate, ciliate; distal tooth of the terminal leaflet always narrower and shorter than adjacent ones; accessory leaflets. Inflorescence compound dichasium with aborted epipodium including the terminal flower, of variable length, sub-to super foliar, 4 to 15 cm. Flowers subdiecious with plants growing in separate, or interspersed male, female, or hermaphrodite colonies; pistillate flowers 16.3(13.0-20.0) mm wide; staminate flowers 19.7(15.0-24.0). Calyx green rarely regular with 5 lanceolate sepals and 5 bractlets, frequently irregular, with 11 or 12 sub-equal parts. Petals white, usually 5 rarely 4 or 6, depressed obovate to very widely obovate, entire, emarginate, or unequally-bilobed, partially overlapping or not; Stamens about 0.5 mm long, protruding above sub-reflexed corolla; hermaphrodite flowers 23.1(17.0-30.0.) mm wide. Pollen grains about 34 µm air dried with longitudinal ridges (Type 1, Staudt 2009). Pistils light yellow, numerous, 1mm long, the group centrally located within the flower as attached to receptacle about 3(3-4) mm. Receptacle in Fruit shape variable from globose, subglobose, to ellipsoidal, and irregular; fruit set may be irregular, poor, or sometimes full, 1.0(0.5-1.2)cm wide $\times 1.5(1.0-1.75)$ cm long; fruit skin ripens red; fruit flesh white, juicy and sweetish, with flat to sour flavor. Achenes sometimes set in pits; length ~ 1.56 mm; ovary vasculature prominent on surface; lateral stylar edge frequently concave, forming a comma-shape. Chromosome number: 2n = 10x = 70(Nathewet et al. 2010; Hummer et al. 2011).

Differs from F. chiloensis and F. xananassa nothosp. cuneifolia by leaves not thick and coriaceous, not reticulate-veiny beneath. Differs from F. vesca subsp. bracteata by leaves usually slightly bluish green, and distal tooth of terminal leaflet always shorter than adjacent teeth as compared with leaves Kelly green and distal



Fig. 1. Fragaria cascadensis Hummer. Collected by K.E. Hummer 2111 (OSC) (PI 664460) from USA, Oregon, Lane Co., NFBR 5897 near Waldo Lake, Oakridge vicinity. Southern exposure, disturbed area at forest edge, along roadside ditch, altitude 1433 m, 6 August 2011.

tooth of terminal leaflet usually longer than adjacent teeth. Differs from F. virginiana subsp. platypetala by leaves with adaxial, scattered, appressed white hairs (~1 mm) and achenes frequently comma-shaped, lateral stylar edge concave as compared with adaxial leaf surface glaucous and achenes dome-shaped with straight lateral stylar edge. The distribution range is in the western Oregon Cascades at elevations from 1,000 to 3,800 m. Differs from all sympatric congeners by the decaploid chromosome number (2n = 10x = 70), whereas F. vesca subsp. bracteata is (2n = 2x = 14) and F. virginiana subsp. platypetala is (2n = 8x = 56).

Representative specimens: U.S.A. OREGON. Deschutes Co.: Carpenter Mountain, jct. Blue River and Lookout Trails, J.F. Franklin 425 (OSC); Marshall Cabin, South Mount Hood, L.F. Henderson 13831(ORE); Pole Bridge, O.L. Ireland 2481 (OSC); South Entrance, Crater Lake Park, L. Wynd 2021(OSC). Hood River Co.: Hood River, H.S. Jackson s.n. (OSC); McKenzie Pass, L.F. Henderson 16829 (OSC). Jefferson Co.: Abbot Butte Spring Road, K.C. Swedberg 79 (OSC). Lane Co.: US NFDR 5897 leading to Waldo Lake, K. Hummer 2102 (OSC) 2104 (OSC) 2105 (OSC); US NFDR 5897 leading to Waldo Lake, K. Hummer 2104 (OSC); US NFDR 5897 leading to Waldo Lake, K. Hummer 2104 (OSC); US NFDR 5897 leading to Waldo Lake, K. Hummer 2105 (OSC); 2 mi above Alder Springs Campground, McKenzie Hwy, O.R. Ireland 592 (OSC). Linn Co.: Hoodoo Butte, M.M. Thompson 95003 (OSC); Hoodoo Butte, M.M. Thompson 95025 (OSC); Hoodoo Butte, M.M. Thompson 95072 (OSC); Sandy Spring, McKenzie Pass Summit, L.E. Detling 3242 (OSC); Santiam Highway, M Cook s.n. (OSC); Tombstone Prairie, H.M. Gilkey s.n. (OS

Specimens maintained as living clones in greenhouses at USDA ARS NCGR: U.S.A. OREGON. Clackamas Co.: Mount Hood National Forest, Burnt Lake Trail, 45.35070, -121.80290, Pl 551794; Mount Hood National Forest, Burnt Lake Trail, Clackamas Co., 45.35572, -121.79338, CFRA 2061. Deschutes Co.: Pacific Crest Trail, E of Big Lake, 44.34548, -121.86743, Pl 551518. Douglas Co.: edge of Umpqua National Forest, western edge of Diamond Lake, 43.18259, -122.13815, CFRA 2084; edge of Umpqua National Forest, western edge of Diamond Lake, 43.18720, -122.15496, CFRA 2085; edge of Umpqua National Forest, western edge of Diamond Lake 43.18579, -122.15921 CFRA 2086; Rogue River National Forest, Oregon Rte. 62. 43.18579, -122.34467, CFRA 2088. Klamath Co.: Deschutes National Forest, Princess Creek Campground, Klamath Co., 43.58628, -122.00952, CFRA 2068. Lane Co.: Willamette National Forest, entrance road to Waldo Lake 43.61872, -121.82260, CFRA 2065; Willamette National Forest, entrance road to Waldo Lake, 43.61872, -121.82260, CFRA 2065; Willamette National Forest, entrance road to Waldo Lake, 43.61872, -122.07930, CFRA 2066. Willamette National Forest, Gold Lake Nordic Area Road entrance, 43.60542, -122.04697, CFRA 2067. Linn Co.: 4 mi S of Santiam Pass, E of



Fig. 2. Fruit of Fragaria cascadensis Hummer. collected by K.E. Hummer 2111 (PI 664460) from USA, Oregon, Lane Co., Waldo Lake Entry Road, NFDR 5897, 6 Aug 2011.

Big Lake, 44.37065, -121.86562, PI 551527; E of Big Lake, Pacific Crest Trailhead, 44.37933, -122.08560, PI 658460; W of Big Lake, 44.37766, -121.87058, PI 657862; W of Big Lake, 45.37766, -121.87058, PI 657865; W of Big Lake, 44.37442, -121.87445, PI 657863; W of Big Lake, 45.41302, -122.087546, PI 657867.

Etymology.—This species is named for the Oregon Cascade Mountains.

Common name.—I suggest Cascade strawberry.

Distribution and habitat.—Populations of Fragaria cascadensis occur at elevations of 1,000 m to 3,800 m, to the west of the divide in the Oregon Cascade Mountains; from the Columbia River in the north, to the southern and western vicinity of Crater Lake in the south. This region is referred to as the "high peaks" (Alt & Hyndman 2009). Habitat: open alpine meadows, or on forest path edges, where direct sunlight breaks through the canopy; along stream banks or in roadside drainage ditches; growing in sandy-clay loam of volcanic origin. At these locations the dominant vegetation is usually Douglas fir [Pseudotsuga menziesii (Mirbel) Franco] or silver fir [Abies amabilis (Douglas ex Louden) Douglas ex Forbes]. Associated plants include: Gaultheria humifusa (Graham) Rydb., Epilobium ciliatum Raf., Lupinus latifolius J. Agardh., Montia parvifolia (Mociño ex de Candolle) Greene, Vicia americana Muhl. ex Willd., Hieracium albiflorum Hook., Artemisia ludoviciana Nutt., and Agoseris grandiflora (Nutt.) E. Greene. The soils have udic moisture and frigid soil temperature regimes. The mean annual precipitation in the northern part of the decaploid distribution range is 200 to 250 cm (Franklin & Dyrness 1973), but it is 100 cm or lower in the southern area.

Phenology.—Fragaria cascadensis begins growing after snowmelt in late May or early June, flowering in early July, about 2–3 weeks later than F. virginiana subsp. platypetala (Rydb.) Staudt at lower elevation below 1,000 m. Runner production begins after flowering. Fruit is ripe during August for about 2 weeks with plants at ≥ 1,500 m elevation ripening 1 to 2 weeks later than those at 1,000 m.







Fig. 3. Achenes of a) Fragaria vesca subsp. bracteata (PI 551813, CFRA 464, near Lost Lake, Oregon); b) F. cascadensis Hummer. (PI 664461, CFRA 2112, Big Lake Road, Oregon), and c) F. virginiana subsp. platypetala. (PI 551553, CFRA 176, near Prineville, Oregon). Bars represent 1 mm.

DISCUSSION

Congener Sympatry

Throughout much of Oregon, *F. virginiana* subsp. *platypetala* and *F. vesca* subsp. *bracteata* (A. Heller) Staudt are sympatric (Staudt 1999; Cook & Sundberg 2011). Sample collection for this study confirmed this frequent sympatry as well as that of *F. vesca* subsp. *bracteata* with *F. cascadensis* at locations near Mt. Hood, Hoodoo Butte, Iron Mountain, and Echo Mountain trail (Hummer et al. 2011).

From physical examination of native living plants at 17 locations from Mt. Hood through Crater Lake where *F. cascadensis* was present, no sympatric octoploids, or other plants of intermediate ploidy, as determined by flow cytometry, were observed (Hummer et al. 2012). However, three plants collected by L. Wynd (numbers 2020 for two plants and 2021 for one plant) in 1928, near the south entrance of Crater Lake, which were mounted together on a single herbarium sheet (OSC 46316), comprise two congeners: two plants with adaxial leaf surfaces that were glabrous and third plant with scattered leaf hairs (with hand written annotation by the collector on the hairs of that specimen). Although the collector originally determined that the pressed specimens on the sheet were one species despite the differential occurrence of the hairs, these specimens can now be re-interpreted as two *F. virginiana* subsp. *platypetala* plants and one of *F. cascadensis*, growing in sympatry near Crater Lake. The occurrence of diploid *F. vesca* subsp. *bracteata*, and octoploid *F. virginiana* subsp. *platypetala* in sympatry with each other and separately with decaploid *F. cascadensis* supports the idea that these taxa may have progenitor-descendant relationship.

Combination of morphological traits

Fragaria cascadensis has some morphological traits similar to those of *F. virginiana* subsp. *platypetala* and others more like those of *Fragaria vesca* subsp. *bracteata*. From several meters away, leaf and inflorescence morphology of the *F. cascadensis* is similar to that of *F. virginiana* subsp. *platypetala*, which is how this species escaped notice until recently. A defining difference is the presence of scattered appressed white hairs about 1 mm long on the adaxial leaf surface of *F. cascadensis*. This trait differs from the smooth, glabrous adaxial leaf surface of *F. virginiana* subsp. *platypetala*, but is similar to that of *F. vesca* subsp. *bracteata*, which has scattered to dense appressed, adaxial leaf surface hairs.

Another morphological difference separating Fragaria cascadensis from F. virginiana subsp. platypetala is achene shape. Some of the achenes of the Cascade strawberry are comma-shaped, having a concave lateral stylar edge, while those of F. virginiana subsp. platypetala are tear-drop shaped. The lengths of the achenes of F. cascadensis and F. virginiana subsp. platypetala are similar, 1.56–1.85 mm, and achenes of both species tend to be longer than those of F. vesca subsp. bracteata, which are about 1.37–1.56 mm long (Staudt 1999). Achenes of F. vesca subsp. bracteata frequently have a persistent style, while those of the other two taxa do not.

Inflorescence lengths of Fragaria virginiana subsp. platypetala are often short, usually shorter than the

foliage. The inflorescence length in *F. cascadensis* is variable within a population, ranging from 4 to 15 cm and from shorter to taller than the foliage. That of *F. vesca* subsp. *bracteata* tends to be taller than the foliage.

1) Ploidy and Genetic Features

Decaploidy in *Fragaria cascadensis* was confirmed by chromosome counts and flow cytometry (Nathewet et al. 2010; Hummer et al. 2011, 2012). The Cascade strawberry has more alleles and more unique alleles (Njuguna 2010) than do octoploid strawberry species *F. virginiana* or *F. chiloensis*. A previous report of high genetic variation in *F. viriginiana* subsp. *platypetala* (Hokanson et al. 2006) partly resulted from the unknowing inclusion of three decaploid *F. cascadensis* samples (CFRA 101, CFRA 110, and CFRA 440) in that study.

Potential Progenitors

With a significant combination of morphological traits, *F. cascadensis* seems strongly linked to both *F. vesca* subsp. *bracteata* and *F. virginiana* subsp. *platypetala*. The facultative outcrossing of *F. vesca* subsp. *bracteata* and the findings of Dermen and Darrow (1938) and Njuguna et al. (2010) suggest that the direction of a hybridization event would likely be *F. vesca* subsp. *bracteata* (or a polyploid derivative) as the mother, and *F. virginiana* subsp. *platypetala* (or a derivative) as the pollen parent, if there was a direct cross. Reports summarized by Dermen and Darrow (1938) and Darrow (1966) indicated that autotetraploids arising from a diploid as mother, with the pollen of higher ploidy cytotypes, could produce a successful cross. The reciprocal cross (with pollen from autotetraploid *F. vesca*) was unsuccessful in the laboratory (Dermen & Darrow 1938). This is, however, counter to Bringhurst's (1990) discussion of the origin of the California *F. xbringhurstii* Staudt pentaploids. These genotypes have arisen from natural crosses of *F. chiloensis* with autotetraploid *F. vesca* subsp. *californica* (Cham. & Schltdl.) Staudt (Bringhurst 1990; Staudt 1999). Future work comparing plastid single nucleotide polymorphisms between the putative parents and *F. cascadensis* could determine the maternal parent.

2) Previously unrecognized cytotype

This unusual cytotype was overlooked by many studying *Fragaria* taxonomy. Other than the decaploid chromosome number, *F. cascadensis* appears similar to the octoploid *F. virginiana* subsp. *platypetala* as described by Staudt (1999). Close inspection is needed to see the morphological differences of hairy adaxial leaf surfaces and comma-shaped achenes. Therefore, *F. cascadensis* has gone unnoticed. Darrow (1966) who collected strawberries and performed many ploidy experiments including synthetic development of multiple levels of polyploidy was unaware of wild *Fragaria* species with more than 56 chromosomes. Hancock et al. (2001) and Harrison et al. (1997) extensively studied octoploid *F. virginiana* Mill. and *F. chiloensis* Losinsk. from North America, including *F. v.* subsp. *platypetala* from the Western Cascade Range of Washington, where all individuals are octoploid. Hokanson et al. (2006) unknowingly included three decaploid cytotypes (CFRA 101, CFRA 110, and CFRA 440) in their analysis, but assumed them to be octoploid.

3) For the present study, 23 OSC herbarium specimens were determined to be *F. cascadensis*, judging from adaxial leaf surface hairs and western High Cascades localities of origin. An additional 16 were determined as *F. vesca* subsp. *bracteata*, judging from adaxial leaf surface hairs, inflorescence length, leaf dentation (size, location, and number per leaf) and collection locality. Strawberry specimens at the OSC herbarium were reviewed and annotated by Staudt. His (Staudt 1999) described the upper leaf surface of *F. virginiana* subsp. *platypetala* as "smooth" based on his studies of strawberries from the Pacific North Western North America. With the definition of *F. cascadensis* sp. nov., I suggest that "smooth and glabrous" is a more appropriate description for the adaxial leaf surface of *F. virginiana* subsp. *platypetala*.

IDENTIFICATION KEY FOR WILD FRAGARIA IN OREGON

Leaves thick to somewhat thick, coriacious, strongly to not strongly reticulate-veiny beneath, superior surface dark g to bluish green; achenes large to medium; plants coastal to inland.	reen
2. Leaves thick, coriacious, strongly reticulate-veiny beneath, superior leaf surface dark green; achenes large (me	an =
1.76, range 1.43-2.04 mm long); plants coastal	F. chiloensis
 Petioles, peduncles, pedicels and runners with appressed-ascending hairs, occasionally macroscopically alr glabrate 	most subsp. lucida
3. Petioles, peduncles, pedicels and runners with spreading, usually dense hairs	subsp. pacifica

2. Leaves somewhat thick, coriacious, not-strongly reticulate-veiny beneath sometimes bluis	sh green to slightly glaucous;
achenes medium (mean = 1.4, range 1.33-1.75 mm long); plants coastal to inland	F. xananassa nothosubsp. cuneifolia
	(Nutt. ex Howell) Staudt
 Leaves not thick and coriacious, not reticulate-veiny beneath, superior surface bluish green; mm long); plants inland. 	achenes smaller (~ 1.37–1.56
4. Leaves bright green; leaflets ovate or obovate to slightly rhomboidal; distal tooth of te than adjacent teeth; teeth ~ 38 or more per leaf; flowers ~ 20 mm in diameter; inflores flowers perfect, sometimes gynodioecious; calyx generally regular with 5 larger sepals at times 11 or 12 merous; calyx mostly reflexed from ripe fruit; achenes ~ 1.37–1.60 mm long	cence usually above foliage; nd 5 smaller bractlets, some-
aristate style	F. vesca subsp. bracteata
4. Leaves green to bluish green; leaflet shape variable, elongated to obovate, cuneiform distal tooth of terminal leaflet usually shorter than adjacent teeth; usually teeth ~ 27 per diameter; inflorescence usually lower than foliage or variable length; plants sub-dio mostly 11 or 12 merous with equal length lanceolate members; calyx clasping or mostly ~ 1.56(1.28–1.85) mm or longer, style not persistent.	leaf; flowers ~ 20–30 mm in ecious; calyx sometimes 10
 Adaxial leaf surface glabrous; achenes generally tear-drop shape, about 1.5 mm long Coast Range, in the Willamette Valley and on eastern side of the divide of the Oregon 	Cascades; elevations gener-
ally < 1,000 m; plant octoploid $(2n = 8x = 56)$	F. virginiana subsp. platypetala
 Adaxial leaf surface with appressed scattered white hairs (~ 1mm); achenes frequently of stylar edge, sometimes tear-drop shaped; distribution in western high Cascade Mountain vicinity in the north to Crater Lake vicinity in the south; elevations of 1,000 m to 3,800 	ains in Oregon from Mt. Hood m; plant decaploid $(2n = 8x)$
= 70)	F. cascadensis

CONCLUSIONS

Fragaria cascadensis, sp. nov., the Cascade strawberry, occurs in the western Oregon High Cascade Mountains. Fragaria cascadensis is visually similar in plant, inflorescence, and most traits of leaf morphology to F. virginiana subsp. platypetala octoploids as described by Staudt (1999). However, the decaploids also share two key characters with F. vesca subsp. bracteata, including adaxial leaf hairs and predominantly comma-shaped achenes.

We provide a cautionary note to breeders who wish to enhance the octoploid strawberry gene pool from wild North American material. If decaploids are inadvertently used in breeding programs in lieu of octoploids, crosses are possible but the resulting enneaploid progeny would have reduced fertility. As an example, a lower fecundity was observed in second generation crosses from Staudt et al. (2009) of *F. iturupensis* (a species since shown to be decaploid) with *F.* × ananassa cultivars (octoploid). From additional scattered sampling of wild *F. virginiana* subspecies across North America (Hummer et al. 2011), decaploid zones, other than the one in the Oregon High Cascade Mountains, have not been detected. However, detailed collection and examination of ploidy is warranted where native diploids and octoploids are sympatric congeners.

Fragaria cascadensis presents the possibility for developing and breeding a new class of cultivated straw-berries at the decaploid level. The wild Oregon decaploids, the Kurile decaploid, F. iturupensis (Hummer et al. 2009), and cultivars of the artificial species F. xvescana (Bauer 1993) may be inter-fertile, because of their equivalent ploidy. Recently Japanese breeders reported on new synthetic decaploids that included genes from the aromatic diploid F. nilgerrensis Schltdl. ex J. Gay (M. Morishita, pers. comm. 2012). Crossing within the decaploids should produce fertile offspring. Perhaps new flavors or resistant genes could be available to consumers from cultivated decaploid strawberries.

This newly described taxon enforces the view of post-glacial polyploid evolution (Harrison et al. 1997; Hancock et al. 2004; Hokanson et al. 2006) in the North American strawberries—not only with continued gene flow between sympatric octoploids, but with the additional dimension of hybrid combinations between multiple ploidy levels, such as diploids with octoploids.

ACKNOWLEDGMENTS

The support for this project from USDA ARS CRIS 5358-21000-038-00D is gratefully acknowledged. The author thanks Kenton L. Chambers for comments on the diagnosis; Nahla Bassil and Wambui Njuguna for genomic information; Tom Davis, Aaron Liston, Jim Oliphant, for frank discussions of data interpretation; Sugae Wada for photographic assistance; and Tom Davis and Daniel Porter for helpful reviews.

REFERENCES

- ALT, D.D AND D.W. HYNDMAN. 2009. Roadside geology of Oregon. Mountain Press Publishing Co., Missoula, Montana.
- BAUER, A. 1993. Progress in breeding decaploid Fragaria xvescana. Acta Hort. 348:60-64.
- COOK, T. AND S. SUNDBERG (EDS.). 2011. Oregon vascular plant checklist. [Rosaceae]. http://www.oregonflora.org/checklist. php. Accessed [2011-10-31].
- DERMEN, H. AND G.M. DARROW. 1938. Colchicine-induced tetraploid and 16-ploid strawberries. Proc. Amer. Soc. Hort. 36:300–301.
- Darrow, G. 1966. The strawberry. Holt, Rinehart and Winston, New York, New York, USA.
- Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service. General Technical Report PNW-8. Seattle, Washington.
- HANCOCK, J.F., P.W. CALLOW, A. DALE, J.J. LUBY, C.E. FINN, S.C. HOKANSON, AND K.E. HUMMER. 2001. From the Andes to the Rockies: native strawberry collection and utilization. HortSci. 36:221–225.
- Hancock, J.F., S. Serçe, C.M. Portman, P.W. Callow, and J.J. Luby. 2004. Taxonomic variation among North and South American subspecies of Fragaria virginiana Miller and Fragaria chiloensis (L.) Miller. Canad. J. Bot. 82:1632–1644.
- Hokanson, K.E., J.M. Smith, A.M. Connor, J.J. Luby, and J.F. Hancock. 2006. Relationships among subspecies of New World octoploid strawberry species, *Fragaria virginiana* and *Fragaria chiloensis*, based on simple sequence repeat marker analysis. Canad. J. Bot. 84:1829–1841.
- HARRISON, R.E. J.J. Luby, G.R. Furnier, and J.F. Hancock. 1997. Morphological and molecular variation among populations of octoploid *Fragaria virginiana* and *Fragaria chiloensis* (Rosaceae) from North America. Amer. J. Bot. 84:612–620.
- HUMMER, K.E., N. BASSIL, AND W. NJUGUNA. 2011. Fragaria. Chapter 2. In: C. Kole, ed. Wild crop relatives: genomics and breeding resources, temperate fruits. Springer WCR Series Vol. 6:17–44.
- HUMMER, K., N. BASSIL, J. POSTMAN, AND P. NATHEWET. 2012. Chromosome numbers and flow cytometry of strawberry wild relatives. Acta Hort. (accepted; in press).
- HUMMER, K., P. NATHEWET, AND T. YANAGI. 2009. Decaploidy in Fragaria iturupensis (Rosaceae). Amer. J. Bot. 96:713-716.
- Nathewet, P., K. Hummer, Y. Iwatsubo, K. Sone, and T. Yanagi. 2010. Karyotype analysis in wild diploid, tetraploid and hexaploid strawberries, Fragaria (Rosaceae). Cytologia 75:277–288.
- NJUGUNA, W. 2010. Development and use of molecular tools in Fragaria. Oregon State University, Corvallis. (Thesis).
- NJUGUNA, W., A. LISTON, R. CRONN, AND N. BASSIL. 2010. Multiplexed *Fragaria* chloroplast genome sequencing. Acta Hort. 859:315–321.
- STAUDT, G. 1989. The species of Fragaria, their taxonomy and geographical distribution. Acta Hort. 265:23-24.
- STAUDT, G. 1999. Systematics and geographic distribution of the American strawberry species: taxonomic studies in the genus *Fragaria* (Rosaceae: Potentilleae). Univ. Calif. Publ. Bot. 81:1–162.
- STAUDT, G. 2009. Strawberry biogeography, genetics and systematics. Acta Hort. 862:71-83.
- STAUDT, G., S. Schneider, P. Scheewe, D. Ulrich, and K. Olbricht. 2009. Fragaria iturupensis: a new source for strawberry improvement? Acta Hort. 842:479–482.